

rate, but different patterns, over time is not difficult (Fig. 2). Smoothing the responses over tens of milliseconds (low-pass filtering below 30 Hz) preserves all the stimulus-related information that is available in the unsmoothed responses (Heller et al., 1995). Including this slow variation in the response accounts for about 25% more information than that in the response strength alone (Optican, Richmond, 1987; Richmond et al., 1990; Tovee et al., 1993; Heller et al., 1995; Victor, Purpura, 1996).

The latency of a response, that is, the delay with which a change in the stimulus elicits a change in firing rate, is considered a particularly important feature of rate modulation. Giawne et al (1996) showed that the latency is strongly related to the contrast or luminance of the stimulus. Recently, we confirmed this result with other stimuli, including gratings (Fig. 3) (Wiener et al.,

1998). The minimum latency at V1 is related to the contrast across all response strengths.

The minimal description of neuronal responses must include some representation of the rate modulation. Whether the rate modulation must be represented at a precision greater than the tens of milliseconds described above continues to be a subject of study.

Exactly Timed Spike Patterns

So far we have seen that both the spike count (including its distribution) and the slowly varying pattern of rate change (including latency) are related to the stimulus. Each carries information that is unavailable from the other. It is also natural to represent a neuronal response as a series of discrete spike arrival times.

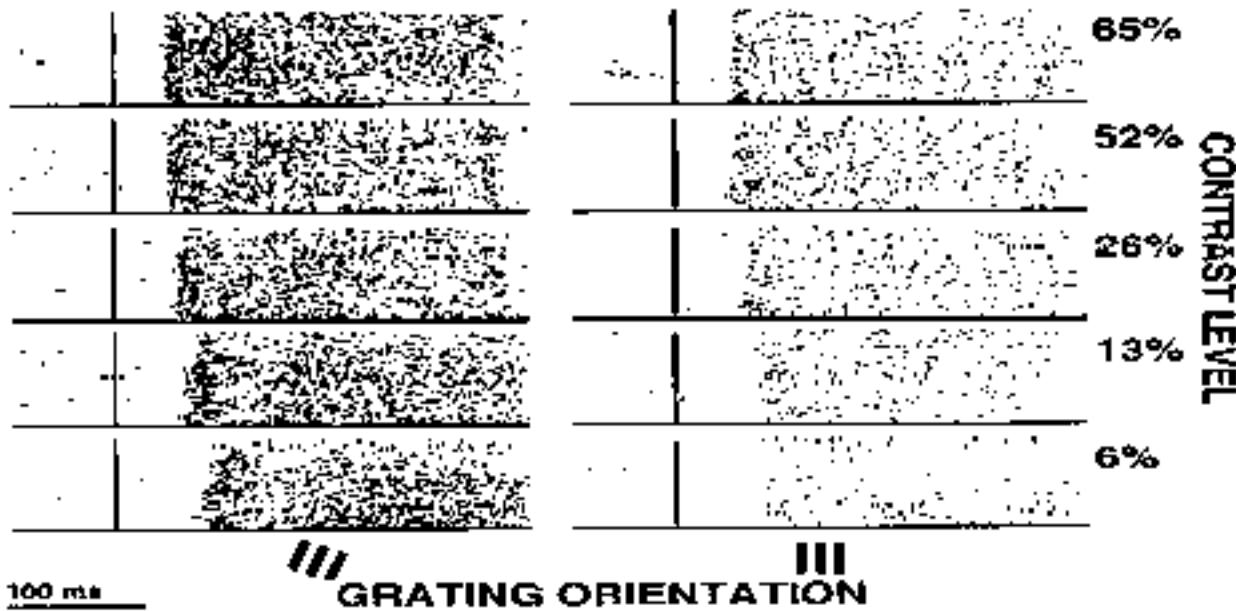


Fig. 3. Responses elicited by gratings of several contrasts at optimal and nonoptimal orientations from a V1 complex cell. There are substantial changes in response strength induced by changes in orientation, whereas the latency changes by, at most, a small amount. The latency becomes substantially longer (~30 ms in this example) as the contrast decreases. The minimum latency at each contrast is the same at both orientations. The response elicited by the lowest contrast optimally oriented grating is large with a long latency (bottom-left column) whereas the response elicited by another grating is weak and has a short latency (top-right column). Thus, latency and response strength are independent